



Gatekeepers to the effects of climate warming? Niche construction restricts plant community changes along a temperature gradient[☆]

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ABSTRACT

Organisms that modify the environment (niche constructors) are likely candidates to mediate the effects of climate warming. Here we assess tundra plant community changes along a temperature gradient and how these are modified in the presence of the common allelopathic dwarf shrub *Empetrum nigrum* and the large herbivore *Rangifer tarandus*.

We developed a structural equation model based on data from a field-based study of 1450 tundra plant communities across Northern Fennoscandia, covering a temperature gradient of 3.5 °C, contrasting *Rangifer* densities, a range of *Empetrum* abundances in addition to gradients in topography and bedrock.

We found temperature to be a significant positive predictor of *Empetrum*, herbaceous and woody plant abundances. However, the effect of temperature as predictor for herbaceous plant abundance was significantly reduced in communities with *Empetrum* present. For woody plant abundance *Empetrum* was a stronger predictor than temperature. In comparison, we found *Rangifer* density to have marginal or no effect on either herbaceous or woody plant abundance. These findings were not modified by either topography or bedrock.

Results from this study indicate that herbaceous plant responses to climate warming are currently reduced in communities where *Empetrum* is present, whereas the abundance of *Empetrum* and other woody plants is promoted. Results also indicate that any future *Empetrum* encroachment is likely to drive tundra communities towards slower process rates and lower biodiversity. As such our results substantiate the importance of understanding the dynamics of niche constructor species and include them in predictive models of climate change.

1. Introduction

The tundra is changing (e.g. Chapin et al., 2005; Elmendorf et al., 2012b; Wookey et al., 2009), with the potential to become more species rich and greener under climate warming (e.g. Aerts et al., 2006; Epstein et al., 2012; Kullman, 2010; Rustad et al., 2001). Environmental modification by organisms, also termed niche construction or ecosystem engineering (Odling-Smee et al., 2013), may, however modify effects of climate warming. Plants can modify the environment in tundra plant communities, for instance by changing nutrient cycling rates (Bråthen and Ravolainen, 2015), subsequently causing plant-based cascade processes that enhance or reduce responses to climate change (Wookey et al., 2009). In addition, herbivores can counteract the greening process (shrub encroachment into circumpolar or alpine areas) (Den Herder et al., 2008; Olofsson et al., 2009; Post, 2013; Ravolainen et al., 2014; Zamin and Grogan, 2013), and hence prevent plant-based cascade processes. The trajectory of change under climate

warming may therefore be dependent on the niche constructing abilities of plants and herbivores inhabiting the tundra.

Plant species are tracking their temperature niche as indicated by the upward and northward changes in species distributions in response to a warming climate (Chen et al., 2011; Klanderud and Birks, 2003; Lenoir et al., 2008). A thermophilization of the tundra flora is happening, where warm adapted species replace cold adapted species (Elmendorf et al., 2015; Gottfried et al., 2012). Because warm adapted species are benefited under climate warming and because the species richness is larger among warm adapted species, an increase in species richness is expected (Kullman, 2010). Yet, at the plot scale, no significant increase in species richness has happened in tundra areas in 30 years, whereas there have been changes in the height and abundance of growth forms (Elmendorf et al., 2012b) with increases described for shrubs, graminoids and forbs (Elmendorf et al., 2012a). Shrubs, in particular, are already common in tundra ecosystems (Walker et al., 2005), and are increasing with recent observed climate warming (Elmendorf et al., 2012b; Myers-Smith et al.,

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2011). However, how this increase in shrub abundance is linked to community species richness and abundance of other growth forms is not evident. Theoretically, shrub encroachment can cause a range of possible outcomes for plant communities depending on the ecological context (Wookey et al., 2009) and empirical evidence of decreasing (Klein et al., 2004; Mod et al., 2016; Post, 2013; Wilson and Nilsson, 2009), stable (Pajunen et al., 2011) and increasing (Bråthen and Lortie, 2016) species richness of vascular plants as a response to shrub encroachment has been found. To advance in the understanding of how ecological contexts influence responses of plant communities to climate warming, large-scale studies on dominant shrub species within a range of habitats and contexts are needed (Christie et al., 2015).

The evergreen dwarf-shrub *Empetrum nigrum* (crowberry) has strong niche constructing capacity (*sensu* Matthews et al., 2014) as indicated by its ability to modify ecosystem properties (Bråthen and Lortie, 2016; Nilsson and Wardle, 2005; Tybirk et al., 2000; Wardle et al., 1998). *Empetrum* is tightly linked to variation in species diversity of tundra plant communities under both high and low intensity *Rangifer tarandus* (reindeer) land use (Ravolainen et al., 2010). The abundance of *Empetrum* has repeatedly been found negatively related to species richness of vascular plants in tundra communities (Bråthen and Lortie, 2016; Bråthen and Ravolainen, 2015; Mod et al., 2016; Wilson and Nilsson, 2009). Accordingly, *Empetrum* is found to be an important predictor along with temperature in species distribution models (Pellissier et al., 2010) and in plant community models (Le Roux et al., 2014). However, although allelopathic to other plant species at their seedling state (González et al., 2015), *Empetrum* does not always have negative effect on coexisting plants. Whereas *Empetrum* is competitively superior to forb and grass species (Mod et al., 2014; Pellissier et al., 2010; Wilson and Nilsson, 2009), it seems to have facilitative effects for species with higher leaf dry matter content (Mod et al., 2014; Pellissier et al., 2010). *Empetrum* may thus modify the environment, thereby driving selection for species with traits causing slow nutrient process rates (cf. Wilson et al., 1999), and potentially reinforcing the filtering effect that *Empetrum* has on the species pool. This is especially pertinent to herbaceous species in tundra plant communities.

Dendroecological studies indicate *Empetrum* is sensitive to climate change (Buntgen et al., 2015; Myers-Smith et al., 2015), and empirical evidence indicates that *Empetrum* is advancing in altitude and abundance in tundra areas in response to recent climate warming (Felde et al., 2012; Klanderud and Birks, 2003; Wilson and Nilsson, 2009). Such observations of a positive response to warming are corroborated by experiments (Buizer et al., 2012; Kaarlejärvi et al., 2012; Wada et al., 2002), and indicate shrub encroachment by *Empetrum* is promoted by climate warming. However, *Empetrum* has been found to be vulnerable to extreme climatic events during winter (Bokhorst et al., 2008) and to attacks by the *Empetrum*-specific parasitic fungus *Arwidssonina empetri* under increased snow cover (Olofsson et al., 2011). Still, *Empetrum* has been found resilient to simulated strong winter damage (Aerts, 2010), has a high tolerance to ice encasement (Preece et al., 2012; Preece and Phoenix, 2014), and it appears that *Empetrum* is relatively resistant to a range of environmental changes, including fertilization, as compared to coexisting species (Tybirk et al., 2000). Hence, although *Empetrum* has been found to be vulnerable to some aspects of climate warming, it seems it mostly thrives.

Empetrum abundance is also affected by herbivores. For instance, close to fences that separate *Rangifer* migration areas, trampling can be intense (Moen and Danell, 2003). As *Empetrum* is vulnerable to trampling (Bell and Tallis, 1973), this can result in reduced abundance (Olofsson et al., 2001; Väisänen et al., 2014). Small rodents have also been shown to control *Empetrum* abundance (Olofsson et al., 2009; Olofsson et al., 2012), but a longer time collapse in small rodent cycles (Ims et al., 2008), may have reduced the capacity of small rodents to do so. Furthermore, while most studies indicate that herbivory are counteracting the encroachment of shrub species, there are empirical indications of *Empetrum* responding differently and that it is rather promoted by *Rangifer* activities (Bråthen et al., 2007b; Francini et al., 2014;

Ylänne et al., 2015). Such promotion can potentially happen through apparent competition because *Empetrum* leaves have low palatability (Tybirk et al., 2000) and through endozoochory because *Empetrum* berries are eaten by e.g. *Rangifer* (Bråthen et al., 2007a). Hence, *Empetrum* seems to be both positively and negatively affected by the activities of herbivores.

In sum, an assessment of how *Empetrum* itself is affected by increasing temperatures and *Rangifer* density, and how *Empetrum* affects tundra plant communities in this context, is likely to yield insight into the development of tundra plant communities under climate warming. Therefore, in this study, we ask to what extent *Empetrum* and *Rangifer* are likely candidates for mediating effects of climate warming in tundra plant communities. We use a space for time approach to address climate warming effects (Blois et al., 2013; Elmendorf et al., 2015): the study design covers a temperature gradient of 3.5 °C across a total of 1450 randomly chosen tundra plant communities in the Fennoscandian part of the circumpolar dwarf shrub tundra (*sensu* Walker et al., 2005). The communities are defined as where plant species share a habitat or environment (*sensu* Daubenmire, 1968). *Empetrum* varies in abundance across these communities, from being absent to subordinate and to having supreme dominance. The study design concomitantly covers ten district pairs of high vs. low intensity of *Rangifer* husbandry land use, and has previously been used to assess effects of *Rangifer* density on the ecosystem state of the tundra communities (Bråthen et al., 2007b), focusing on mammalian herbivore abundances (Ims et al., 2007) and plant diversity (Bråthen and Lortie, 2016; Bråthen and Ravolainen, 2015). In this study we hypothesize that (1) *Empetrum* abundance increases along the temperature gradient, and that (2) higher *Rangifer* densities promote *Empetrum* abundance at higher temperatures. We also hypothesize that (3) *Empetrum* reduces the effect that increasing temperatures has in promoting both inflorescences and biomass of growth forms with higher process rates such as forbs and grasses. In addition, since higher *Rangifer* densities have already been shown to reduce biomass of forbs and grasses as well as the abundance of inflorescences (Bråthen et al., 2007b), we hypothesize that (4) *Rangifer* counteract any positive effect of temperature on the abundance of herbaceous plants. Furthermore we hypothesize that (5) *Empetrum* and increasing temperatures facilitate the biomass of other shrub species, but that (6) higher *Rangifer* densities do not modify this relationship because the abundance of these growth forms is mostly independent of *Rangifer* densities (Bråthen et al., 2007b). In order to test these hypotheses in a comprehensive way we developed a structural equation model, and then we tested each hypothesis separately.

2. Materials and methods

2.1. Study area

Field work for this study was conducted in the coastal alpine tundra of northern Fennoscandia between latitudes 69.2–71.2°N and longitudes 20.5–31.3°E (Fig. 1). This is a region characterized primarily as dwarf-shrub tundra (Walker et al., 2005), with *Empetrum nigrum* being both the most common shrub and the most dominant plant (Bråthen et al., 2007b; Ravolainen et al., 2010). The region is typically snow covered until late June and the main vegetation types are heath, meadows and marshes. Besides *Empetrum*, heath is dominated by the dwarf shrubs *Betula nana*, *Salix herbacea*, *Vaccinium myrtillus*, *V. vitis-idaea* and *V. uliginosum*. Forb and grass-rich meadows are often populated with *Bistorta vivipara* and *Viola biflora*, *Avenella flexuosa*, *Deschampsia cespitosa*, *Anthoxanthum nipponicum*, and sedges of *Carex* spp. Marshes are dominated by *Eriophorum angustifolium* and *E. vaginatum* along with various species of *Carex*. *Empetrum* is often present in both meadows and marshes. Plant names follow the Pan-Arctic Flora (<http://nhm2.uio.no/paf/>). The main large herbivores in this region are the migratory, semi-domestic *Rangifer tarandus* that have their summer pastures along the coast, which is divided into districts to facilitate

management. Other common herbivores include moose (*Alces alces*), domestic sheep (*Ovis aries*), and small rodents (Ims et al., 2007).

The study region is characterized by steep climatic gradients from west to east as well as from coast to inland, caused by the warm NE Atlantic Current that gradually declines from west to east (see temperature map in Fig. 1). The northernmost coast of the study region is classified as Arctic (Walker et al., 2005). Average summer precipitation (June, July and August) is 65, 54 and 48 mm in the west, middle, and east of Finnmark, respectively (calculated from Norwegian Meteorological Institute, <http://www.eklima.no>). The coastal part of the study region is furthermore characterized by variable bedrock (mainly gabbro in the west, slate and sandstone towards the east [Geological Survey of Norway, <http://www.ngu.no/>]).

2.2. Study design

A total of 1450 plant communities were sampled within the borders of ten pairs of neighbouring *Rangifer* districts (Fig. 2), where each pair represents two decades of high versus low *Rangifer* densities (official numbers provided by the Norwegian Reindeer Husbandry Administration <http://www.reindrift.no/>) (Bråthen et al., 2007b). Different *Rangifer* densities are to a large extent determined by spatiotemporally heterogeneous management practices in *Rangifer* husbandry (Tveraa et al., 2007). Faeces counts in the field confirmed that each pair of neighbouring *Rangifer* districts represented a contrast in low and high *Rangifer* density (Bråthen et al., 2007b).

Sampling within the *Rangifer* districts was based on *a priori* stratification and plant community selection using GIS as well as on rules set *a priori* to the field sampling (*sensu* Mörsdorf et al., 2015). Each *Rangifer* district was covered with a 2 × 2 km grid (in which each cell is referred to as a “landscape area”). For each district, and in order to avoid landscape areas dominated by glaciers, lakes and boulder fields, satellite image classifications of vegetation types (Johansen et al., 1995) were evaluated to identify landscape areas with more than the district average of mesic and wet vegetation. Among these, landscape areas were retained unless they included > 50% forest, lakes, sea, glaciers or included a fence or a major road (based on <http://www.norgeskart.no/>). The final landscape areas within each *Rangifer* district were selected randomly. The number of selected landscape areas increased as a function of district area, with the final number of selected landscape areas per district ranging from 6 to 14 units.

The choice of plant communities within the selected landscape areas was random. The landscape areas were subdivided into 100 potential sampling squares of 200 m × 200 m, with a maximum of 21 randomly selected squares (Fig. 1). The centre of each selected square was the starting position for a 50 m long transect whose direction was determined by a random GPS position on a circle with a 50 m radius. If any of the transects had to be discarded because of steep terrain, water (lake, large river or very wet mire), snow cover (more than a 5 m section of the transect running through snow), boulder field (more than half of the transect running over boulders devoid of vegetation), or the transect was below the tree-line, another random direction or start position was identified. If no new acceptable transect placement within the area was available, the entire sampling square was discarded. Each transect was sub-sampled at plots every 5 m along the transect with a triangular sampling frame with sides of 40 cm. Each transect constituted a tundra plant community (Fig. 1). All landscape areas were sampled in July and August 2003. Each landscape area was sampled by two individuals but for a few areas sampled by one person. To avoid differences due to plant phenology, *Rangifer* districts belonging to the same pair were analyzed simultaneously, and sampling was conducted from west to east as the season progressed in order to sample at or just after peak growing season.

2.3. Environmental variables

A downscaled WorldClim temperature layer (“Warmest Quarter” Hijmans et al., 2005) of 100 m × 100 m resolution (Pellissier et al., 2013) was applied for average summer temperatures (Fig. 1). We used average summer temperature (across June, July and August) because it is physiologically more meaningful to alpine species than other temperature variables (Körner, 2003).

Bedrock types for each plant community were obtained from maps provided by the Geological Survey of Norway (<http://www.ngu.no/>). The bedrock type was classified as poor (0), e.g. quartzite, moderate (1) e.g. amphibolite, and rich (2) e.g. mica or limestone, in providing nutrients available to the plant community as based on Tarbuck and Lutgens (1992).

A curvature index, i.e. a geodaphic factor that serves as a surrogate for the moisture level of vegetation (Moore et al., 1991), was calculated per plant community using GIS and a digital terrain model of 25 m × 25 m pixels (<http://www.kartverket.no>). Index values from 1 to −1 indicate concave to convex curvature, i.e. moist to dry terrain, respectively. Visual inspection in the field of a few sites verified that the index values correctly depicted concave or convex terrain.

2.4. Biological variables

In each plot the point intercept method (Bråthen and Hagberg, 2004) – using three pins attached to the corner of the triangle (Fig. 1) – was used to obtain measures of above ground live vascular plant species biomass. Prior to further analyses, point intercept data per species and plot were converted to biomass estimates in units of grams per m² using established calibrations (Ravolainen et al., 2010). To achieve estimates of growth form biomasses and total biomass per plant community, the data were summed across species and averaged across all plots. Point intercept data on inflorescences (including all inflorescence parts and all their phenological stages) were registered separately, and were summed across species and averaged across all plots to achieve estimates of inflorescences abundance per plant community. Estimates of *Empetrum* biomass and *Empetrum* berry abundance were calculated separately.

2.5. Data analyses

Structural equation models were developed in the R environment version 3.2.3 (<http://www.r-project.org>) using in the lavaan package (Rosseel et al., 2013). Data were screened for distributional properties and nonlinear relations which resulted in several variables being log-transformed. The first structural equation model was exploratory, built to test the effect of all predictor variables (temperature, *Rangifer* density, curvature and bedrock) onto the abundance of herbaceous and woody growth forms. The possible mediating effect by the abundance of *Empetrum* was included in the model by having *Empetrum* both as a response variable and as a predictor to the plant growth form abundances. All non-significant predictors were successively removed from the model. The final model was selected based on parsimoniousness and goodness of fit as interpreted from Chi Square tests, RMSEA and Comparative Fit Index provided in the lavaan package (Rosseel et al., 2013). The contribution of each predictor variable in the final model was then assessed in order to possibly simplify the model further. Final models with one predictor variable removed at a time were compared to the final model using anova model comparison. The final model including all predictors had the best AIC score. Lastly, the final model was tested for whether the hierarchical setup of the study design had any consequences to the variance explained by the model using the lavaan survey package and by an assessment of the robust Chi Square test (Oberski, 2014). At this stage, all predictors were retained in the model, including predictors that became non statistically significant but still explained variance above a value of 0.04. Variance explained by the different predictor variables was obtained from model outputs as

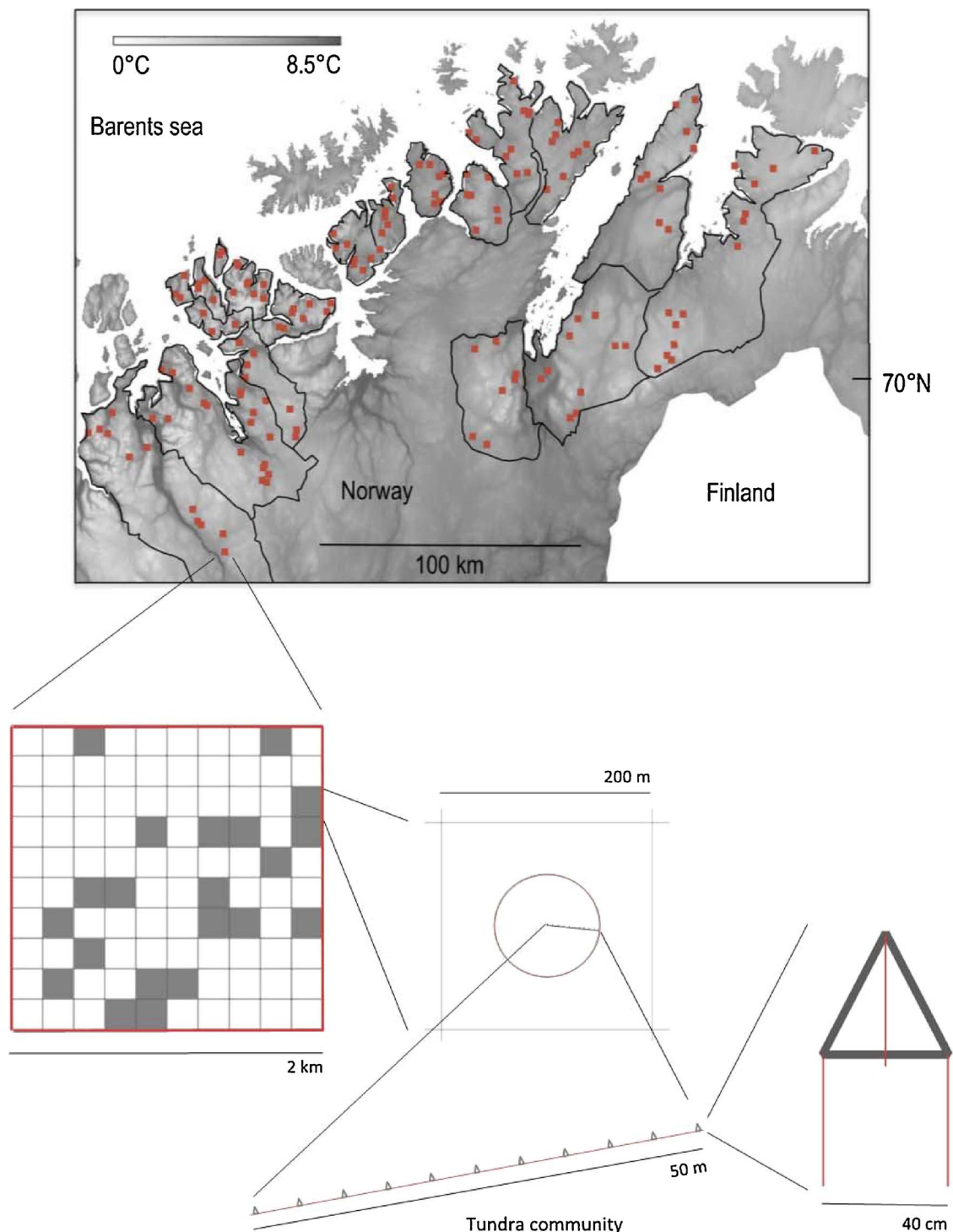


Fig. 1. Summer temperatures across northern Fennoscandia including landscape areas where plant communities were analyzed (upper panel) and an overview of the study design applied in each landscape area (lower panel). In the upper panel the borders represent the 20 *Rangifer* husbandry districts and the red squares represent the landscape areas. In the lower panel the nested design for each landscape area, geographically positioned a priori to the field season, is shown. Within each landscape area a random set of maximum 21 squares of 200 m × 200 m were analyzed by running a transect from the square centre in a random direction. Plots were regularly placed along each transect representing a plant community and each plot was analyzed by the point intercept method using three pins. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

standardized values, and manually entered into a path diagram of the final structural equation model.

In addition we developed linear mixed effects models (Pinheiro and Bates, 2000) using the nlme package in R to test specific hypotheses. In the first set of models fixed factors were *Empetrum* biomass and *Empetrum* berries as response variables and temperature and *Rangifer* density (high and low) as predictor variables. For the model on *Empetrum*

berries *Empetrum* biomass was also a predictor. In a second set of models fixed factors were species richness, the abundance of inflorescences, and the biomass of each growth form as response variables along with temperature, *Empetrum* biomass and *Rangifer* density as predictor variables. For all models the random factors were landscape areas nested in pairs of *Rangifer* districts.

To achieve homogeneity of the residual variance of models, all

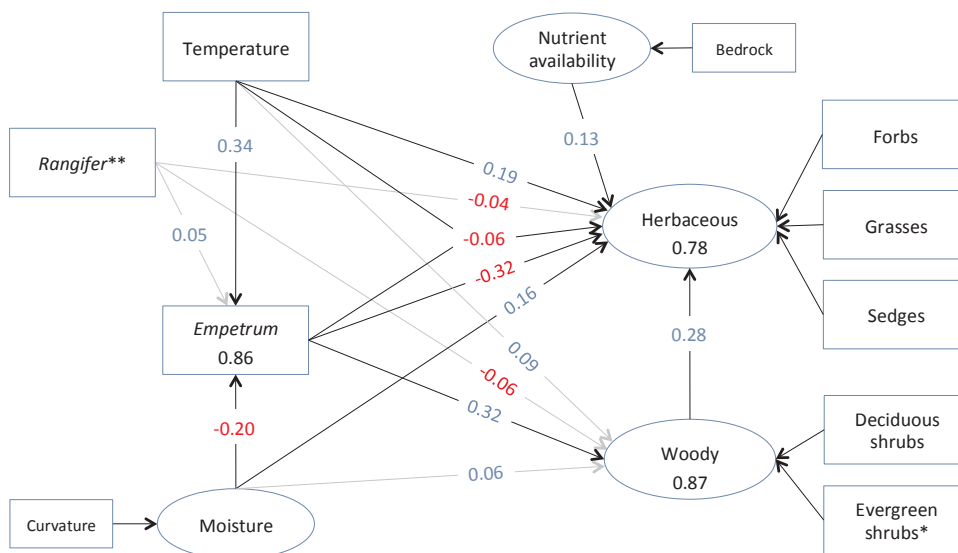


Fig. 2. Structural equation model representing connections between *Empetrum*, temperature, *Rangifer* and herbaceous and woody growth forms supported by the data. Blue text represents positive effects, red text represents negative effects. Black arrows indicate significant effects, grey arrows indicate effects no longer significant under the adjustment of the model when accounting for the hierarchical study design. Only the interaction term significant in both models is presented: the interaction between *Empetrum* and temperature on herbaceous biomass. Model test statistic = 4.825, with 2 model degrees of freedom and $p = 0.090$ (indicating close model-data fit). The robust test statistic = 1.138 (model also considering the hierarchical design), with 2 model degrees of freedom and $p = 0.566$ (again indicating close model-data fit). Comparative Fit Index = 0.996 and Root Mean Square Error of Approximation = 0.031, further indicate close model fit. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

*excluding *Empetrum*

**anthropogenically determined

abundance variables (i.e. inflorescence abundances and biomasses) were log transformed ($x + 1$). All predictor variables were standardized (mean = 0 and standard deviation = 1) to facilitate comparison between variables and models (e.g. Iversen et al., 2014).

The standardized coefficients and the confidence intervals of fixed predictors were extracted from model outputs and presented and plotted as predicted values. From the second set of models the predicted values were presented in three different plant community categories; in communities with *Empetrum* biomass constituting 0%, 20–30% or 70–80% out of total community biomass.

All models were extended with nutrient availability (bedrock index) and moisture level (curvature index) as fixed factors to assess any confounding towards main predictors and are presented with their standardized coefficients in supplementary information (Table S1). In addition, standard deviations and confidence intervals of the random factors for each set of models are presented.

3. Results

Empetrum was present in 1230 out of the 1450 randomly chosen tundra plant communities, and composed more than half the biomass across all communities. Among the growth forms, forbs constituted on average the least biomass, followed by sedges, grasses, evergreen shrubs (excluding *Empetrum*) and deciduous shrubs (Table 1). In the communities where *Empetrum* was not present, other shrubs constituted on average 55% of the community biomass.

The structural equation modelling (SEM) showed a significant influence of temperature on the biomass of *Empetrum* and herbaceous plants and a non-significant influence on woody plant biomass (Fig. 2). The influence of *Rangifer* density on either response variable was not significant. The influence by *Empetrum* on herbaceous and woody plant biomass was stronger than that of temperature, but with a negative and a positive relationship respectively. Moreover, there was a significant negative interaction between temperature and *Empetrum* on herbaceous plant biomass, indicating the influence of *Empetrum* was more negative at higher temperatures. Moisture, as presented in the form of the curvature index, had a significant negative influence on *Empetrum* biomass and a significant positive influence on herbaceous plant biomass. Nutrient availability, as presented by the bedrock index, was only influential to herbaceous plant biomass, and in a positive way.

The bivariate model (linear mixed model) result on the influence of temperature on the *Empetrum* biomass was consistent with the SEM results, showing a marked increase in *Empetrum* biomass in response to increasing temperature (Fig. 3, Table 2). However, in contrast to the SEM results, higher *Rangifer* density had significant positive effect on the *Empetrum* biomass in the bivariate model, but with small effect size (Fig. 3, Table 2). The abundance of *Empetrum* berries was only modelled using a bivariate model, with model results showing slightly less berries in communities with high *Rangifer* densities (Fig. 3, Table 2), and a positive relationship with temperature where also the biomass of *Empetrum* was higher (Table 2).

The bivariate model results on the influence of temperature and *Rangifer* on the biomass of the herbaceous and woody growth forms were also mostly consistent with the SEM results; Temperature had a significant positive relationship with both herbaceous and woody plant biomass whereas the effect of *Rangifer* density was insignificant (Fig. 2, Table 2). With increasing biomass of *Empetrum* in the plant communities these positive relationships to increasing temperature were severely reduced for the herbaceous plant biomass, whereas they were enhanced for the woody plant biomass (Fig. 4a, Table 2). This latter interaction effect on woody plant biomass was however not part of the final SEM model (Fig. 2) because the variance explained by the interaction was less than 0.03.

Bivariate models were run to assess responses among the different herbaceous or woody growth forms. The biomass of each of the growth forms were all significantly positively related to the temperature gradient from 4.4 to 7.9 °C (Fig. 4a, Table 2). The effect of *Rangifer* was insignificant for all growth forms except for forbs and grasses where a negative effect of high *Rangifer* densities was similar in effect size and sign to that of *Empetrum* biomass (Table 2).

The bivariate model on the abundance of inflorescences (not including *Empetrum* inflorescences) showed a similar outcome to that of the forbs and grasses, with a positive effect of temperature, a negative effect of *Empetrum* biomass and a negative effect of high *Rangifer* densities (Fig. 4b). The bivariate model on species richness showed a positive effect of temperature and a negative effect of *Empetrum*, but no effect of different *Rangifer* densities (Fig. 4b, Table 2).

The predictor strength and direction of temperature, *Empetrum* biomass and *Rangifer* density was only slightly modified by adding nutrient availability (i.e. bedrock index) and moisture (i.e. curvature

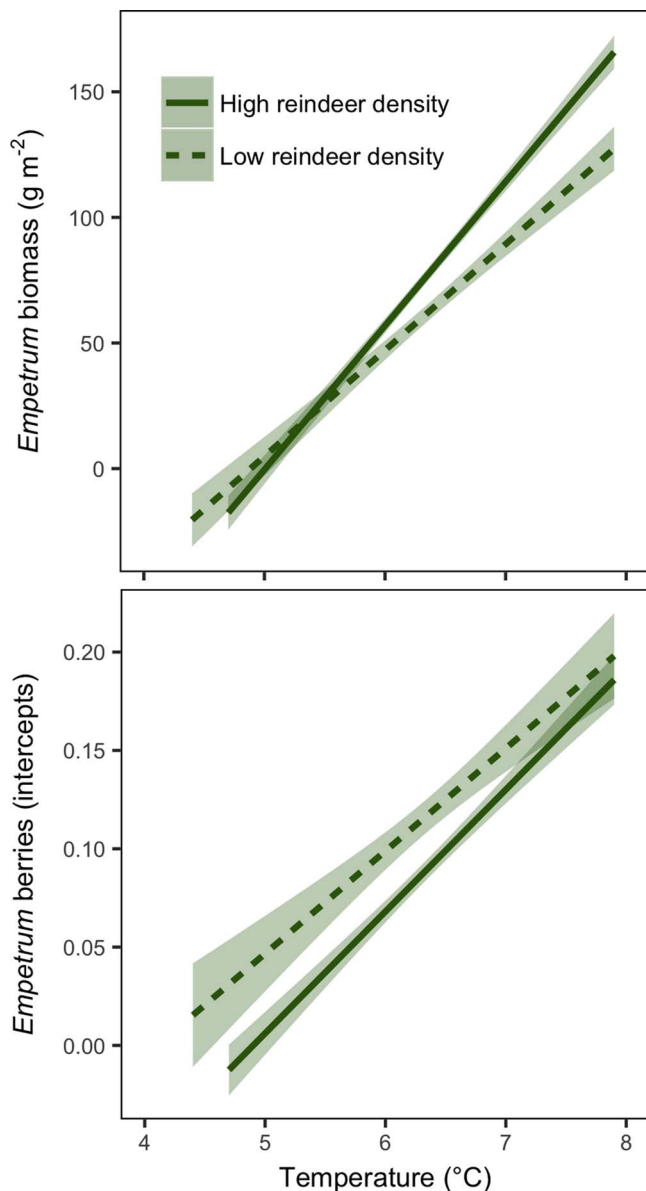


Fig. 3. The effect of increasing temperature (warmest quarter) and *Rangifer tarandus* density (high vs. low) on the predicted values of aboveground biomass (g m^{-2}) and the abundance of berries (point intercept frequency) of *Empetrum nigrum* presented on a $\log_e(x + 1)$ scale. The linear regressions are based on predicted values from a lme model output and are presented with \pm 95% confidence bands.

index) as predictors of community characteristics (Table S1). This indicates there were no confounding effects between main predictors and the additional environmental predictors, and is consistent with the SEM results that showed temperature and *Empetrum* biomass had a clear influence alongside that of the environmental predictors. Such lack of confounding is also strengthened by the fact that the full range of moisture and nutrient availability regimes were present in all categories of *Empetrum* dominance (Fig. S1 and S2). Nonetheless, the nutrient availability was significantly positively related to species richness, herbaceous and woody shrub biomass. Moisture was significantly negatively related to *Empetrum* biomass (indicating more *Empetrum* in convex and hence drier terrain) and significantly positively related to species richness, inflorescence abundance and herbaceous biomass (indicating higher abundances in more concave and hence moister terrain).

4. Discussion

In this study, we assessed the extent to which *Empetrum nigrum* and *Rangifer tarandus*, two species with niche constructing abilities (*sensu* Matthews et al., 2014; Odling-Smee et al., 2013), mediate the response of tundra plant communities to increasing temperatures. We found *Empetrum* – a common dwarf shrub species in circumboreal-polar areas (<http://nhm2.uio.no/paf/>) – to have clear mediating effects whereas we found effects of *Rangifer* – the dominant large herbivore in this ecosystem (Huntington, 2013) – to have no or low mediating effects in comparison. Moreover, we found the biomass of *Empetrum* to be positively affected by increasing temperatures and to be slightly positively affected by higher *Rangifer* densities. Because *Empetrum* has allelopathic capacity its proliferation implies a deterioration of habitats to a range of other organisms (Aerts, 2010; Bråthen et al., 2010; Nilsson et al., 1993; Nilsson and Zackrisson, 1992; Wallstedt et al., 2001), with potential wide-reaching consequences to circumpolar areas.

4.1. *Empetrum* abundance increases with increasing temperatures

The increase in abundance of both biomass and berries of *Empetrum* with increasing temperatures is in line with previous studies assessing *Empetrum* biomass (Felde et al., 2012; Kaarlejärvi et al., 2012; Klanderud and Birks, 2003; Wada et al., 2002; Wilson and Nilsson, 2009) and reproduction (Buizer et al., 2012). The ability of *Empetrum* to acquire nitrogen early in the season (Larsen et al., 2012; Wipf, 2010) may give it a competitive advantage over other plant species when responding to increasing temperatures. Also, the increase in berry abundance likely contributes to increased establishment and hence increased abundance of *Empetrum* under warmer temperatures. Increase in *Empetrum* abundance with warming has been found along a temperature gradient ranging from 5 to 15 °C (Buizer et al., 2012) (i.e. at higher temperatures than that provided in the current study), indicating climate warming can promote encroachment by *Empetrum* in ecosystems also beyond circumpolar regions.

Higher intensity land use by *Rangifer* husbandry had a marginally positive effect on the biomass of *Empetrum*, and is consistent with previous findings (cf. Bråthen et al., 2007b). The positive effect of *Rangifer* herbivory might have parallels to *Empetrum rubrum*, a species found in the southern hemisphere and with a high genetic similarity to *Empetrum nigrum* (Popp et al., 2011). Claims are that grazing by sheep over the last 100 years has turned grasslands into *Empetrum rubrum* dominated heathlands (Collantes et al., 1999). In our system, the process by which herbivory causes *Empetrum nigrum* to gain abundance on behalf of other species is most likely apparent competition because it has both low nutrient content (Kaarlejärvi et al., 2012; Sorensen et al., 2008), phenolic rich leaves (Gallet et al., 1999; Väisänen et al., 2013) and low palatability (Tybirk et al., 2000) even during winter when food resources are scarce (Danell et al., 1994). *Empetrum* has also been found to benefit from endozoochory by *Rangifer* (Bråthen et al., 2007a). Hence, the reduced abundance of *Empetrum* berries at higher *Rangifer* densities may ultimately be part of the positive effect of *Rangifer* densities on *Empetrum* abundance: *Rangifer* is likely dispersing *Empetrum* into new habitats. Areas of high *Empetrum* cover are, however, avoided by *Rangifer* (Iversen et al., 2014) and presence of other herbivores is also negatively linked to areas of high *Empetrum* abundance (as shown in a companion study by Ims et al., 2007). There may thus be a threshold in *Empetrum* abundance at which herbivores are no longer influencing its abundance.

4.2. Climate warming effects on tundra plant communities modified by *Empetrum*

Our finding that the abundances of both inflorescences and biomass of herbaceous and woody plants increased with increasing temperatures in the tundra plant communities is in line with expectations of an

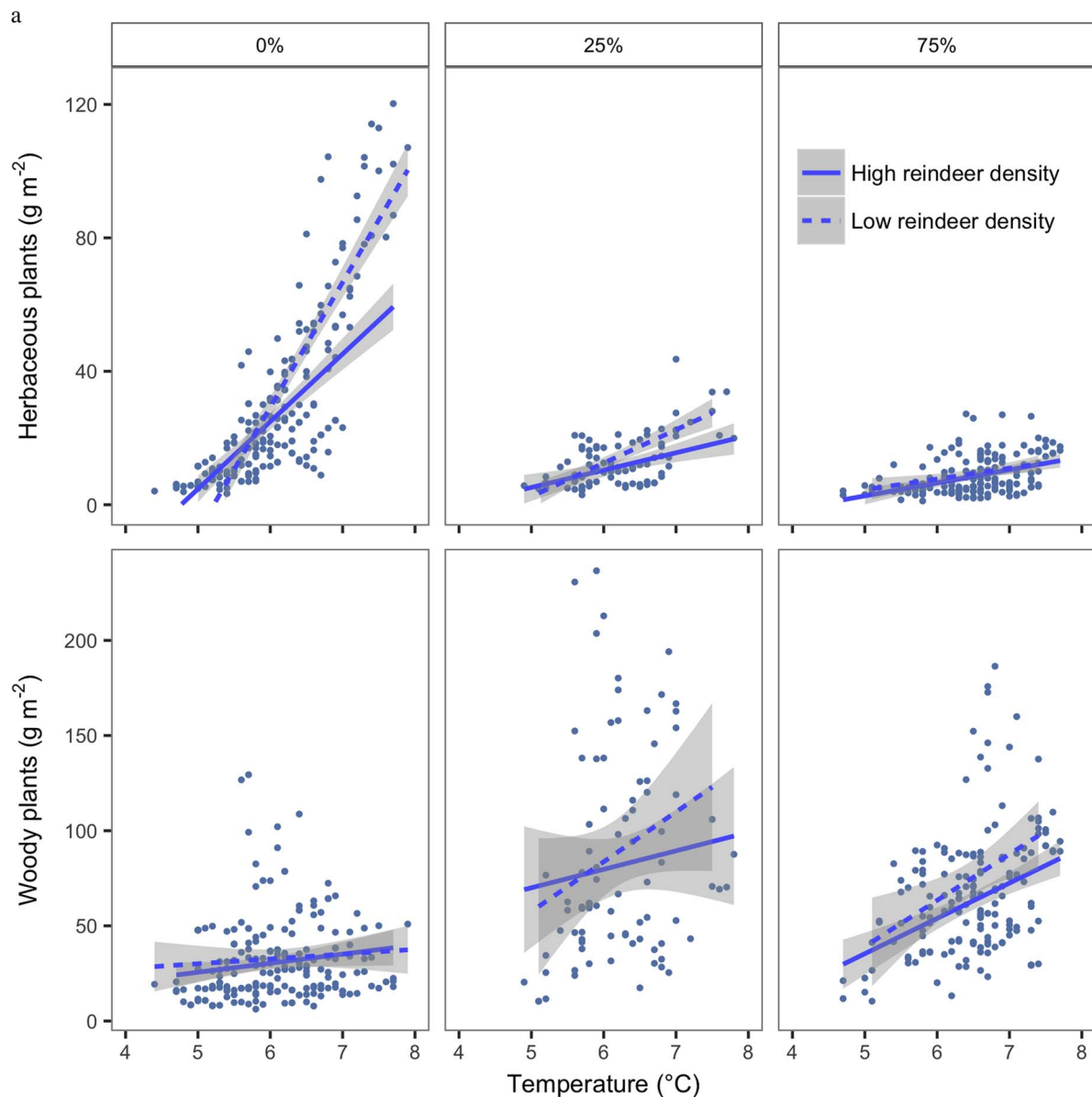


Fig. 4. The effect of increasing temperature (warmest quarter) and *Rangifer tarandus* density (high vs. low) and increasing levels of *Empetrum* biomass on the predicted values of **a**) the aboveground biomass (g m⁻²) of herbaceous (forbs, grasses and sedges) and woody (deciduous and evergreen shrubs) growth forms and on **b**) the abundance of species richness and inflorescences (point intercept frequency) in the plant communities. The three panels represent communities with 0%, 25% (20–30%) and 75% (70–80%) of community biomass occupied by *Empetrum* biomass. All variables are presented on a log_e (x + 1) scale. The linear regressions are based on predicted values from a lme model output and are presented with ± 95% confidence bands.

increase in ecosystem process rates in response to climate warming (Elmendorf et al., 2012a). Increased biomass in general indicates higher productivity. Also an increase in the abundance of inflorescences will likely improve seed availability and new plant establishment because tundra communities often are seed limited (Graae et al., 2011). The biomass of herbaceous plants, the most productive and palatable growth forms (Chapin et al., 1996; Cornelissen et al., 2004; Cornelissen et al., 2007), were more positively related to the increasing temperatures than that of shrubs. However, in communities with *Empetrum* present the strength of temperature as a predictor of higher herbaceous biomass clearly declined. Although herbaceous growth forms utilize different nutrient pools than *Empetrum* (Michelsen et al., 1996), suggesting low direct competition for nutrients, reduced biomass of herbaceous species in the presence of *Empetrum* is likely. That is, recalcitrant evergreen litter can slow warming-induced increases in soil fertility (De Long et al., 2016; Hobbie, 1992). Additionally, forbs and grasses are especially vulnerable to the allelopathic capacity of

Empetrum at their germination and seedling stage (Bråthen et al., 2010; González et al., 2015). It is thus likely that niche construction by *Empetrum*, through modifying habitat quality for herbaceous plants, limits the capacity of herbaceous plants in tundra communities to respond positively to climate warming.

In contrast, the biomass of woody plants, i.e. dwarf shrubs, was positively related to *Empetrum* biomass. Increases in the abundance of shrub species alongside increases in *Empetrum* have been shown in previous climate warming studies in dwarf shrub heaths (Buizer et al., 2012; Kaarlejärvi et al., 2012; Wada et al., 2002). Because shrub species in average are long-lived (e.g. Büntgen et al., 2015), they are likely to be promoted by climate warming at an established developmental stage and are hence not as dependent on the seedling stage previously shown to be vulnerable to *Empetrum* interference (González et al., 2015; Nilsson and Zackrisson, 1992). It may rather be that facilitating effects such as sheltering among established shrubs (Wipf et al., 2006) promote shrub species to further encroach upon the tundra in response to

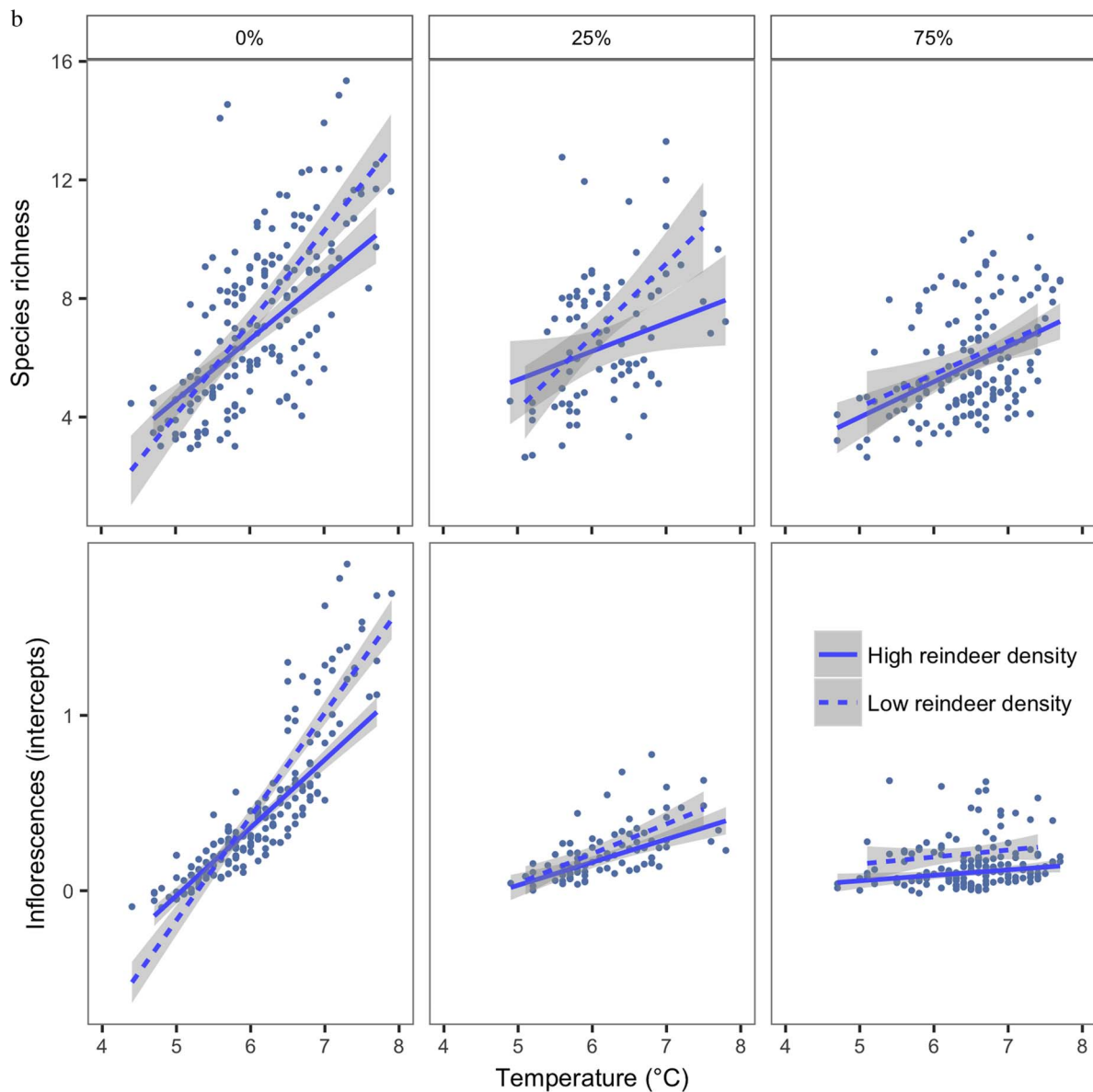


Fig. 4. (continued)

climate warming.

4.3. Climate warming effects on tundra plant communities modified by *Rangifer*

The effects of land use by *Rangifer* husbandry on herbaceous growth forms were on average small in comparison to that of *Empetrum*, but when addressing the herbaceous growth forms individually, both forbs and grasses were found to be negatively affected by both higher *Rangifer* densities and *Empetrum* biomass. Hence, our study supports studies addressing *Rangifer* grazing where a general reduction of forbs (Bernes et al., 2015), a general decline in seed production (González et al., 2010) and a decrease in the forb response to climate warming (Kaarlejärvi et al., 2013), have been found.

4.4. Implications for ecosystem functioning

Niche construction by *Empetrum* can be so strong that the physical removal of the plant itself has no consequence to aboveground species composition or soil abiotic and biotic properties of its habitat even after ten years (Wardle et al., 2012; Wardle and Jonsson, 2013). Such a

legacy effect of *Empetrum* niche construction is plausible due to the bioactivity of leaves accumulated in soil (Bråthen et al., 2010; Wallstedt et al., 2005). *Empetrum* may also have cascading effects on plant-herbivore interactions in tundra ecosystems. For instance, the diet of small rodents consists to a large extent of forbs and grasses (Soininen et al., 2013a; Soininen et al., 2013b), which, as shown in this study, have lower abundance in the presence of *Empetrum*. Also, the reduction of forb and grass biomass at higher *Rangifer* densities (Bråthen et al., 2007b) may come as a consequence of *Empetrum* being a dominant species in most plant communities: The relative grazing pressure on forbs and grasses probably increases when co-occurring with *Empetrum*. Critiques of the ecological sustainability of reindeer husbandry (Moen and Danell, 2003) may thus be valid if they are linked to a trajectory of niche construction by *Empetrum*, promoted by climate warming and more intense *Rangifer* land use, as it may have subsequent cascading effects onto the whole ecosystem.

4.5. Implications for model predictions

Shrub expansion following warming in the Arctic is linked to plant longevity and persistence indicating that model assumptions of fast

Table 1Total and average species pool and aboveground biomass presented per growth form and for *Empetrum nigrum* and in total across the tundra plant communities included in this study.

Growth form	Species pool per growth form	Average species pool (mean \pm SD)	Aboveground biomass (mean g m ⁻² \pm SD)
Forbs	105	1.18 \pm 1.84	5.4 \pm 11.6
Grasses	23	1.34 \pm 1.47	9.1 \pm 17
Sedges	47	1.31 \pm 1.37	7.8 \pm 14.8
Deciduous shrubs	17	2.14 \pm 1.14	63.5 \pm 58.3
Evergreen shrubs*	9	1.02 \pm 0.93	24 \pm 32.4
Vascular cryptogams	21	0.16 \pm 0.44	0.9 \pm 4.0
<i>Empetrum nigrum</i>		0.85 \pm 0.35**	118 \pm 106.6
Total per plant community		8.08 \pm 4.34	228.7 \pm 146.6

* Not including *Empetrum*.** Average presence of *Empetrum* across all plant communities.

response rates to climate warming are overestimated (Büntgen et al., 2015). The identified linkages between shrub expansion and *Empetrum* and *Rangifer* in this study further indicate that model assumptions of climate responses may be overestimated for areas where species with niche constructing capacity are common. *Empetrum* and to some extent *Rangifer*, as results of this study may indicate, improve niches for long-lived shrubs and deteriorate niches for herbaceous plants. In consequence plant longevity and persistence are favoured over higher process rates and short reaction time to climate warming. Such niche construction may also limit the range expansions of southern species into circumpolar areas (Virtanen et al., 2010) as tundra communities will be less suited as stepping-stones to plants tracking their climatic niche. Accordingly, there is lower variability in warm thermal limits in Fennoscandia as opposed to the Alps, as shown for the climatic niches of species common to the Alps and Fennoscandia (Pellissier et al.,

2013). Also, whereas the current assessment of the Arctic acknowledges a controlling impact of herbivores on the encroachment of shrubs under climate warming (Ims et al., 2013), our study shows that the encroachment of a particular shrub, i.e. *Empetrum*, is more likely enforced, although marginally, by herbivory. As such this study substantiates the call for species specific studies on shrub encroachment (Myers-Smith et al., 2011) and further substantiates the conclusion of previous studies to include *Empetrum* (Le Roux et al., 2014; Pellissier et al., 2010) and *Rangifer* (Ims et al., 2013) into predictive models of tundra ecosystem change. In summary, the capacity of *Empetrum* to cause a decoupling with soil processes (Wardle et al., 2012), be unpalatable or avoided by herbivores (Danell et al., 1994; Ims et al., 2007; Iversen et al., 2014) and be competitively superior to herbaceous plants (Mod et al., 2014; Pellissier et al., 2010) suggests that an increase in its abundance is likely to drive a trajectory of tundra communities and ecosystems

Table 2

Standardized coefficients (\pm 95% C.I.) of fixed effects predictors extracted from mixed effects models on community and *Empetrum* characteristics, along with their random factors (SD \pm 95% C.I.). All models include temperature (warmest quarter), *Empetrum* biomass and *Rangifer* density (high vs. low) as predictors along with their significant interactions. The evergreen shrub biomass is not including *Empetrum* biomass, and the inflorescences are not including *Empetrum* inflorescences. Statistically significant predictors have confidence intervals that do not overlap with zero, and non-significant predictors are presented in grey. Growth form names are short for their biomasses, whereas berries and inflorescences are short for their point intercepts.

	Predictors, fixed variables				Random factors	
	Temperature	<i>Empetrum</i> biomass	<i>Rangifer</i> density	Temp x <i>Empetrum</i> bm	District pairs	Landscape areas
Response variables						
<i>Empetrum nigrum</i>						
Biomass	0.642 (0.492, 0.792)	-	0.316 (0.005, 0.627)	-	0.308 (0.123, 0.771)	0.792 (0.658, 0.954)
Berries	0.016 (-0.003, 0.140)	0.066 (0.052, 0.081)	-0.032 (-0.064, -0.0001)	0.023 (0.010, 0.036)	0.043 (0.023, 0.081)	0.052 (0.035, 0.077)
<i>Community characteristics</i>						
Species richness	0.204 (0.159, 0.250)	-0.035 (-0.060, -0.010)	-0.057 (-0.150, 0.035)		0.213 (0.126, 0.362)	0.245 (0.208, 0.288)
Inflorescences	0.083 (0.050, 0.117)	-0.079 (-0.101, -0.056)	-0.080 (-0.142, -0.018)	-0.052 (-0.073, -0.030)	0.066 (0.031, 0.139)	0.139 (0.109, 0.175)
Herbaceous plants	0.446 (0.340, 0.553)	-0.343 (-0.407, -0.278)	-0.137 (-0.346, 0.072)	-0.077 (-0.137, -0.017)	0.307 (0.168, 0.562)	0.527 (0.443, 0.628)
Woody plants	0.281 (0.188, 0.375)	0.299 (0.246, 0.352)	-0.038 (-0.226, 0.150)	0.065 (0.016, 0.114)	0.450 (0.265, 0.765)	0.496 (0.422, 0.583)
<i>Growth forms</i>						
Forbs	0.325 (0.221, 0.428)	-0.236 (-0.295, -0.177)	-0.280 (-0.488, -0.072)		0.403 (0.234, 0.693)	0.545 (0.460, 0.646)
Grasses	0.471 (0.363, 0.579)	-0.136 (-0.201, -0.071)	-0.265 (-0.469, -0.062)		0.210 (0.096, 0.462)	0.504 (0.419, 0.607)
Sedges	0.183 (0.082, 0.283)	-0.289 (-0.352, -0.226)	0.165 (-0.032, 0.363)		0.399 (0.233, 0.681)	0.488 (0.406, 0.587)
Deciduous shrubs	0.320 (0.216, 0.425)	0.200 (0.141, 0.259)	-0.025 (-0.233, 0.184)		0.451 (0.260, 0.785)	0.545 (0.464, 0.641)
Evergreen shrubs	0.192 (0.063, 0.322)	0.596 (0.515, 0.676)	0.006 (-0.222, 0.234)		0.617 (0.369, 1.030)	0.527 (0.425, 0.653)

towards slower process rates and lower biodiversity. Such change may be indicative of ecosystem retrogression (Peltzer et al., 2010; Wardle et al., 2004). As such our results substantiate the importance of understanding the dynamics of niche constructor species and include them in predictive models of climate change.

4.6. Conclusion

In this study, tundra plant community changes along a temperature gradient were clearly modified by the presence of the common allelopathic dwarf shrub *Empetrum nigrum* and modified to a marginal degree by the large herbivore *Rangifer tarandus*. More specifically we found the increase in herbaceous plant biomass with increasing temperature to be reduced in the presence of *Empetrum*, whereas the biomass of woody plants was enhanced. Importantly, we also found the biomass of *Empetrum* to increase with increasing temperature. Higher *Rangifer* density negatively affected biomass of forbs and grasses and abundance of inflorescences, and positively, although to a small extent, *Empetrum* biomass. Based on these results we argue for the inclusion of niche constructor species in predictive models of climate change due to their ecosystem-modifying role.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ppees.2017.06.005>.

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